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Characteristics of the cocoon and natural history of the gregarious *Meteorus restionis* sp. n. (Hymenoptera, Braconidae, Meteorinae) from Costa Rica

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Abstract

A new species of a gregarious *Meteorus* wasp (Braconidae) constructs an unusual cocoon mass. *Meteorus restionis* **sp. n.** is described and distinguished from similar species. Cocoons of *M. restionis* are dark-brown, ovoid, and they are attached perpendicularly by their posterior end along a long, suspended cable. The cable is formed by intertwined, independent threads which are glued together at irregular intervals along its length, suggesting a certain degree of cooperation or at least tolerance among larvae during the construction of the cable. Intertwining and gluing the individual threads in a single cable presumably gives it a greater resistance against wind and other environmental stress. Prior to emergence the wasp cuts a neat, circular cap at the anterior end of its cocoon, and the cap remains attached by some threads to the rest of the cocoon.

Keywords

cocoon traits, gregarious species, sex ratio

Introduction

The purpose of this paper is to describe a new species of the genus *Meteorus* and its uniquely-formed cocoons, recently discovered and observed on the campus of the Universidad de Costa Rica.

Meteorus wasps are koinobiont endoparasitoids primarily of larvae in several Lepidoptera families and, less commonly, of Coleoptera larvae, but no species of *Meteorus* attack both groups (Muesebeck 1923, 1939, 1958; Huddleston 1980, 1983; Maetô 1990; Zitani 2003; Shaw 2006; Stegenberg 2008). Species of this cosmopolitan and highly diverse genus attack especially exophytic caterpillars including Geometridae, Noctuidae, Arctiidae, Pyralidae, Sphingidae, Nymphalidae, Papilionidae, Hesperiidae, Megalypygidae, and Limacodidae (Shaw and Huddleston 1991; Zitani et al. 1998; Shaw and Nishida 2005; Shaw and Jones 2009).

Larvae of *Meteorus* species range from solitary to highly gregarious (Shaw 2006) and they emerge by chewing a hole through the abdomen of the host larva while it is still alive (Zitani et al. 1997; Shaw and Nishida 2005). While most *Meteorus* are solitary parasitoids of small caterpillars, several tropical species are known to be gregarious parasitoids of larger caterpillars (Muesebeck 1939, 1958; Nixon 1943, Zitani et al. 1997, 1998; Zitani 2003, Shaw and Nishida 2005).

Once emerged from an exophytic caterpillar, the *Meteorus* larva moves a short distance from the host and begins the construction of its cocoon on a leaf or twig (Zitani and Shaw 2002). Nearly all species, including some highly gregarious species (e.g., *M. oviedoi* Shaw and Nishida, *M. congregatus* Muesebeck, Zitani et al. 1998), construct their cocoons independently though they may be very close to each other (Zitani and Shaw 2002, Shaw and Nishida 2005). In species with exophytic hosts each *Meteorus* larva produces first a thread whose length varies from a few centimeters to nearly 3 m (Zitani and Shaw 2002), and then constructs its cocoon at the furthest extreme of this thread, where the larva pupates facing downward. However, a few species construct complex communal cocoons (e.g., *M. townsendi* Muesebecki, *M. komensis* Wilkinson) whose larvae apparently cooperate to construct a massive structure, within which each larva produces an independent cocoon (Zitani and Shaw 2002).

Color and shape of cocoons vary across *Meteorus* species. Their color ranges from pale-brown to nearly black and their shape is generally ovoid with either a blunt or a nipple-like anterior end (Zitani and Shaw 2002). In general, *Meteorus* species are especially noted for their diverse silk-spinning and cocoon-forming behaviors (Zitani and Shaw 2002; Zitani 2003; Stegenberg 2008; Shaw and Jones 2009); however, the formation of cocoons discussed in this paper is, as far as is known, unique. Costa Rican *Meteorus* species have been the focus of some recent taxonomic studies (Zitani et al. 1997, 1998; Shaw and Nishida 2005) but many species likely remain still undescribed. Here we describe *Meteorus restionis* sp. n. from Costa Rica, the characteristics of its cocoons, and present some additional information on its biology.

Materials and methods

We (ET and GB) collected two groups of cocoons on the Campus de la Universidad de Costa Rica, San Jose province, Costa Rica (9°54'N, 84°03'W; elevation 1200 m). The campus is located on the western region of the Central Valley where the mean annual precipitation is 1900 mm and the mean annual temperature 20°C, with a dry season from December through March (Bergoeing 1998). There are abundant trees and groups of bushes scattered over the campus. All cocoons were collected, those of one group placed in a plastic bag (cocoons of the second group were all empty), and maintained indoors.

Distance between most cocoons of one group was measured: the first basal 14 cocoons, 13 in the middle section of the cable, and the 13 most distal cocoons. Some of these cocoons were photographed under the dissecting microscope using a digital camera Nikon Coolpix 4500, and then individually measured using the program Image Tool v. 3.0. We additionally quantified the weight supported by all threads together (a cable with a length of 7.5 cm) produced by all larvae in the second group. One extreme of the cable was held with a clip and a small plastic container was hung at the other extreme of the cable. Small beads of lead were one by one added into the container and when the cable broke the beads and the container were weighed. Finally small pieces of individual threads that formed part of the cable were cut, mounted on glass slides, and observed and photographed under the compound microscope.

Specimens were sent to SRS and GZJ for description. Morphological terminology and characters used in this description follow Zitani et al. (1997, 1998), Shaw and Nishida (2005), and Shaw and Jones (2009). Microsculpture terminology follows Harris (1979). Scanning electron microscopy was done at the University of Wyoming Microscopy Core Facility using a Hitachi tabletop scanning electron microscope, model TM-1000. Specimens were examined uncoated at an operating voltage of 15 kV. Acronyms for museum collections are as follows: University of Wyoming, Laramie (ESUW); and Museo de Zoología, Universidad de Costa Rica, San José (MZCR).

Taxonomy

Meteorus restionis **Shaw and Jones, sp. n.**
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Fig. 1

Holotype female (point-mounted), COSTA RICA: San José, UCR campus, 1100 m, 1 October 2007, E. Triana and G. Barrantes, emerged from silk cocoons found on *Monstera* vine growing on *Cordia* tree surrounded by mowed grass. Deposited in ESUW.

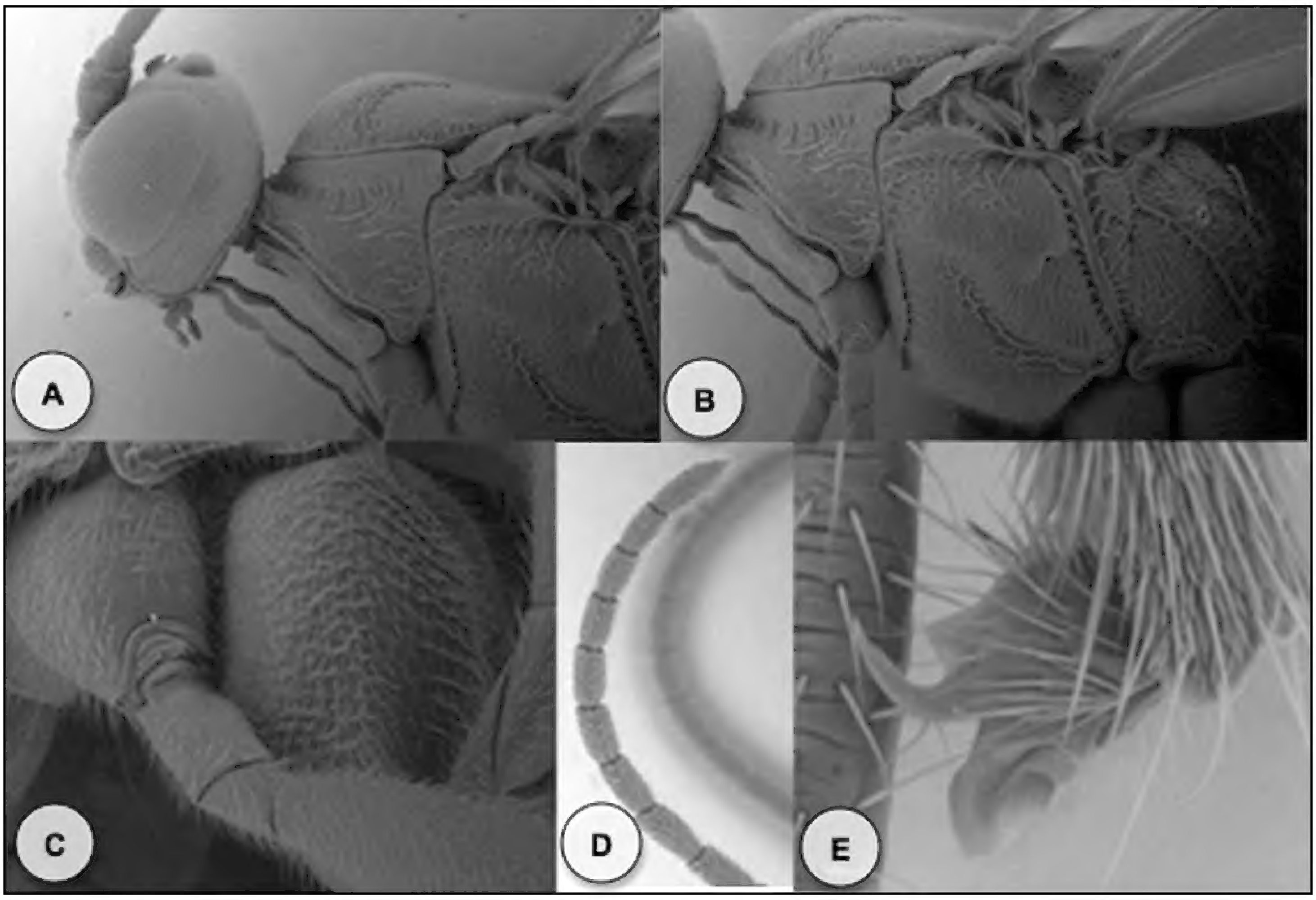

Figure 1. *Meteorus restionis* sp. n., lateral view. **A** Detail of head and anterior mesosoma **B** Detail of mesosoma showing mesopleuron and sternaulus sculpture **C** Middle and hind coxa sculpture **D** Apex of antennal flagellum **E** Hind tarsal claw with basal lobe; part of ovipositor sheath on left.

Paratypes. 16 females, 6 males, same data as holotype, deposited in ESUW; 5 females, 2 males, same data as holotype, deposited in MZCR.

Diagnosis. Mandible strongly twisted, second tooth directly behind first tooth in lateral view; ocelli smaller than OOD, ocello-ocular distance 1.2x ocellar diameter; occipital carina complete; wing membrane clear; vein r ½ length of 3RSa; propodeum areolate-rugose; hind coxa finely rugulose; first metasomal tergite without dorsopes; ventral borders of first tergite joined completely along basal ½ of segment; tergum 2 black laterally, medially with white narrow hourglass-shaped figure.

Description (holotype). Body length = 4.1 mm (Fig. 2A).

Color (Fig. 2A). Body mostly yellowish brown except head orange, compound eye silver, and other parts of body with dark contrasting markings as follows: flagellum and pedicel dark brown; scape and pedicel orangish brown infused with dark brown; ocellar triangle black; dorsal margin of pronotum with black band; lateral lobes of mesonotum and scutellum dark brown to black; mesonotum medially and scutellar disc yellow; metanotum and propodeum black; apical ½ of hind coxa dark brown to black; hind femur apically, hind tibia, and hind tarsi dark brown; wing membrane clear; wing venation and pterostigma dark brown; metasomal tergites 1–3 black dorsally except petiole yellowish white basally in dorsal view, petiole entirely white ventrally, and tergum 2 medially with white narrow hourglass-shaped figure; ovipositor and sheaths dark brown.

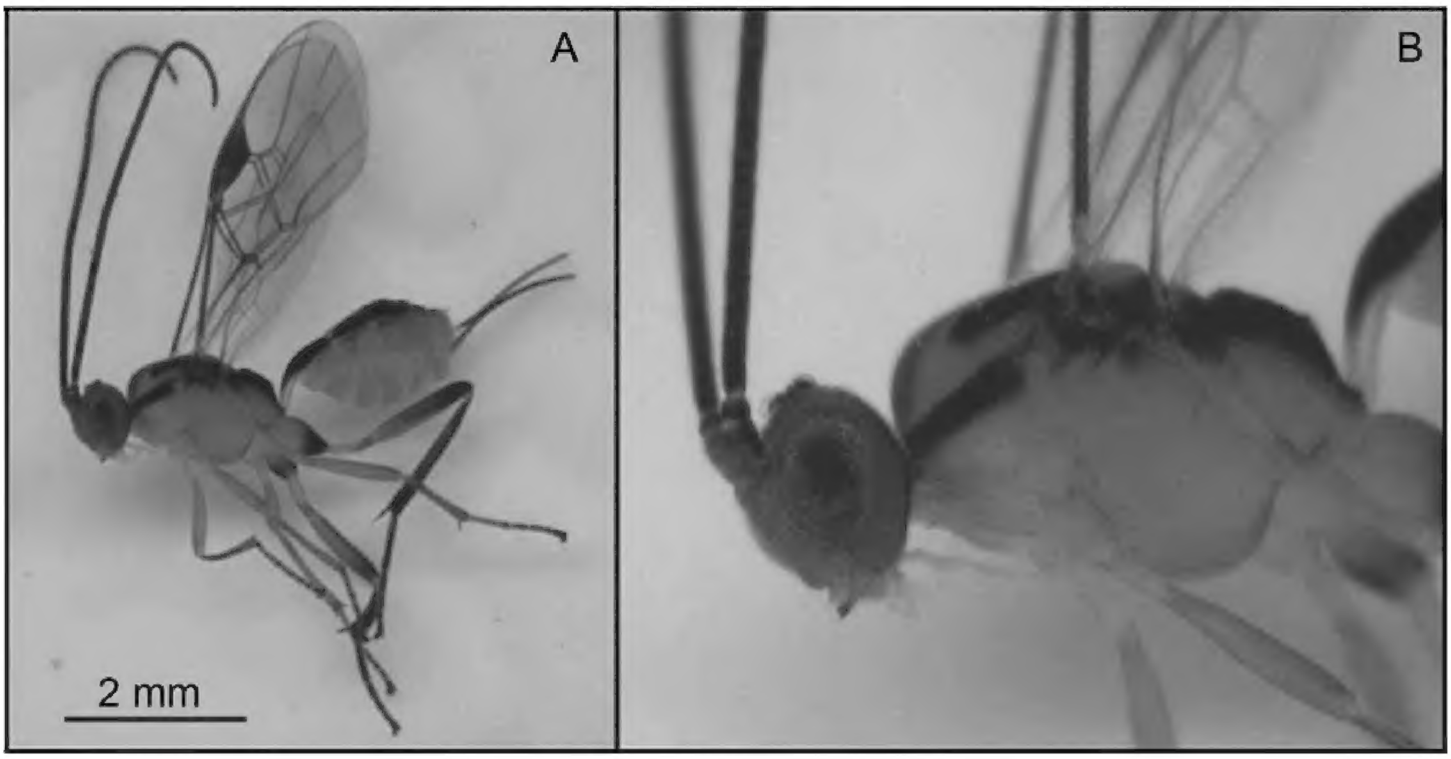

Figure 2. Female *Meteorus restionis*. **A** Pattern of coloration **B** Head details.

Head (Figs 1 and 2B). Antenna with 32 flagellomeres; flagellar length/width ratios as follows: F1 = 3.5; F2 = 3.3; F3 = 3.2; F28 = 2.5; F29 = 2.5; F30 = 2.5; F31 = 2.5; F32 (apical flagellomere) = 4.0; tip of apical flagellomere acutely pointed; head 1.2× wider than high, head height 1.4× eye height; eye small but protuberant, slightly converging ventrally in anterior view; maximum face width 1.1× minimum face width; minimum face width 1.5× clypeus width; malar space length 1.1× mandible width basally; ocelli smaller than OOD, ocello-ocular distance 1.6× ocellar diameter; lower margin of clypeus with fine rugulose wrinkles; mandible strongly twisted; occipital carina complete; vertex, in dorsal view, descending vertically behind lateral ocelli.

Mesosoma. Notauli rugulose, not distinct, and mesonotal lobes not well-defined; scutellar furrow with 1 median carina; mesopleuron polished, punctate; sternaulus weakly rugulose, broad but not long; propodeum areolate-rugose, median depression absent.

Legs. Hind coxa dull, weakly rugulose; larger hind tibial spur about 0.4x as long as hind basitarsus length; tarsal claw with a small blunt basal tooth, strongly curved.

Wings. Forewing length 3.9 mm; vein m-cu amtefurcal; second submarginal cell of forewing slightly narrowed anteriorly; vein r 0.5× length of 3RSa.

Metasoma. first metasomal tergite without dorsopes; ventral borders of first tergite joined completely along basal ½ of segment; first tergite dorsally longitudinally costate on apical half beyond spiracles, costae slightly convergent posteriorly; ovipositor short, thick at base, 1.6× longer than first tergite.

Variation, paratype females. Other females as in holotype except body length 3.9–4.2 mm; forewing length 3.9–4.0 mm; antennae with 31–32 flagellomeres.

Variation, paratype males. Similar to females except body length 3.9–4.0 mm. Antenna with 31–33 flagellomeres. Body color is similar to females except the white medial pattern on tergum 2 is broader and more variable in shape.

Comments. Specimens of *Meteorus restionis* sp. n. were identified by SRS using the key to Costa Rican *Meteorus* species by Zitani et al. 1998. They key, with some difficulty, to couplet 11, where they are nearest to *Meteorus dos* Zitani. This species is distinct from *M. dos* by having smaller eyes, broader face, less convergent eyes, and frons without a strong median tubercle. At couplet 10 *M. restionis* sp. n. is difficult to key because the sculpture on tergum 1 is somewhat intermediate between the sculpturing patterns seen in *M. alejandromasisi* Zitani and *M. dos* Zitani. Although the longitudinal costae of the first metasomal tergite are mostly rather parallel (as in *M. alejandromasisi)* they do converge somewhat posteriorly, so will key onward to couplet 11 near *M. dos*. The only other *Meteorus* species known to reside on the UCR campus is *M. oviedoi* (Shaw and Nishida 2005). Although somewhat similar in overall color pattern, *M. restionis* sp. n. differs from *M. oviedoi* by its shorter OOD and larger ocelli (OOD, ocello-ocular distance, 1.2× ocellar diameter in *M. restionis* and 1.6× ocellar diameter in *M. oviedoi*), and by its very different cocoon-forming behavior (described below).

Etymology. The specific epithet is from the Latin *restionis*, meaning "rope-maker" as a reference to the cocoon-forming behaviour of this *Meteorus* species.

Distribution. All the type specimens were reared from gregarious cocoons collected on campus of the University of Costa Rica, Montes de Oca, San Pedro, San José in Costa Rica. This is the only location where the species has been found, although the associated plants are widespread.

Characteristics of the cocoons. Both groups the cocoons were suspended from a single cable (Fig. 3A), whose entire lengths were 72 cm and 63.5 cm respectively. This cable was formed by individual threads that twisted on each other and intertwined like a rope. In both cases the independent threads were attached to the lower surface of a leaf of a fruit salad vine plant (*Monstera deliciosa*, Araceae) and they intertwined, forming a single cable, about 5 cm beneath the leaf surface. Both fruit salad vine plants climbed trunks of *Cordia eriostigma* trees (Boraginaceae) which were separated by 5 m. One of the cables branched off at 12.5 cm from the end, i.e. dividing the main cable in two; one branch having 19 and the second 11 cocoons. The cable of the other group did not branch and had 49 cocoons. No sign of the possible host larva was found in either case. The cocoons in both cases were grouped at the last section of the suspended cable (14 and 17 cm respectively), and the distance between contiguous cocoons varied from 29 to 0 mm (0 mm when two cocoons were opposite to each other at the same level of the cable). The distance between cocoons decreased toward the tip of the cable (basal section: mean = 26.83 mm, SD = 35.49 mm, N = 14; middle section: mean = 1.65 mm, SD = 2.21 mm, N = 13; distal section: mean = 1.58 mm, SD = 2.21 mm, N = 13).

The cocoons were dark-brown and had an ovoid shape. The posterior end was wider than the anterior end which was blunt, rather than ending with a nipple-like final portion as the cocoons of some other species (Figs 3B–C). All cocoons were attached nearly perpendicularly by the posterior extreme to the suspended cable, rather than to an individual thread (Figs 3A, 4A–B). Prior to emergence the wasps cut a neat,

circular cap at the anterior end of the cocoon, and the cap remained attached by some threads to the rest of the cocoon (Fig. 5A). Inside the cap there was a yellow soft-pad against which the head of the pupating wasp "rested" inside the cocoon (Fig. 5A–B).

Thread resistance. The cable was very resistant to breaking. One of the cables resisted a weight of 44.17 g before breaking. What looked like a single thread, constructed possibly by an individual larva, consisted of two relatively thick threads when observed under the compound microscope and each of these threads were formed by multiple very thin fibrils (Figs 6A–B). Additionally, the fibrils and threads were glued together and at irregular intervals along the cable with large clogs of a resin-like substance that bound several threads together (Fig. 6C).

Wasp emergence and sex ratio. All but one wasp emerged from the first group of cocoons collected (cocoons of the other group were empty). Within this group 22

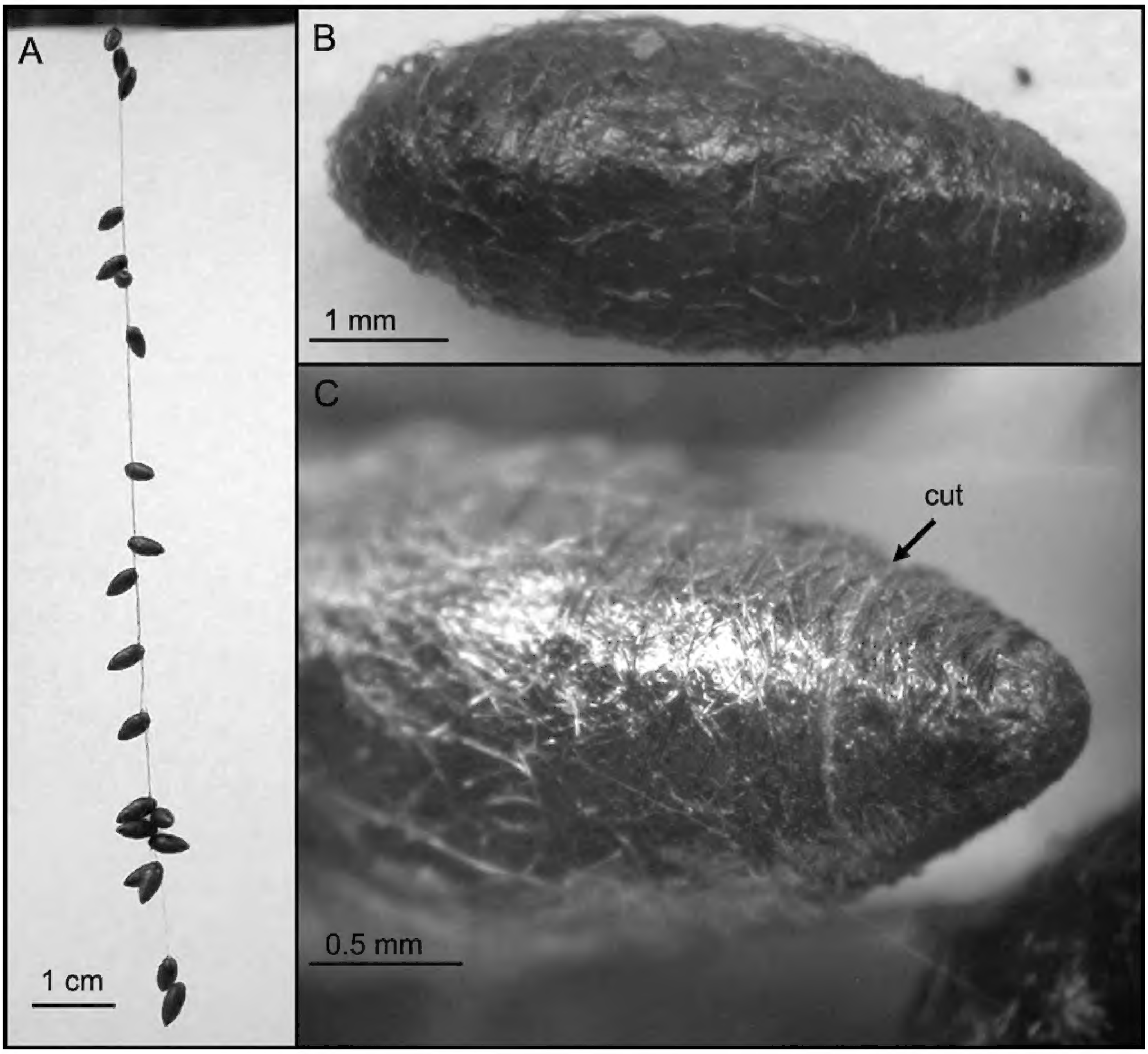

Figure 3. Group and shape of cocoons of *Meteorus restionis*. **A** Distal section of a hanging cable showing 20 of the 49 cocoons in the group. Note the nearly perpendicular position of the cocoons relative to the cable **B** Individual cocoon; note the lack of the nipple-like anterior end typical in cocoons of other species **C** Detail of the anterior end showing its shape and the very fine cut produced for the wasp inside prior to its emergence.

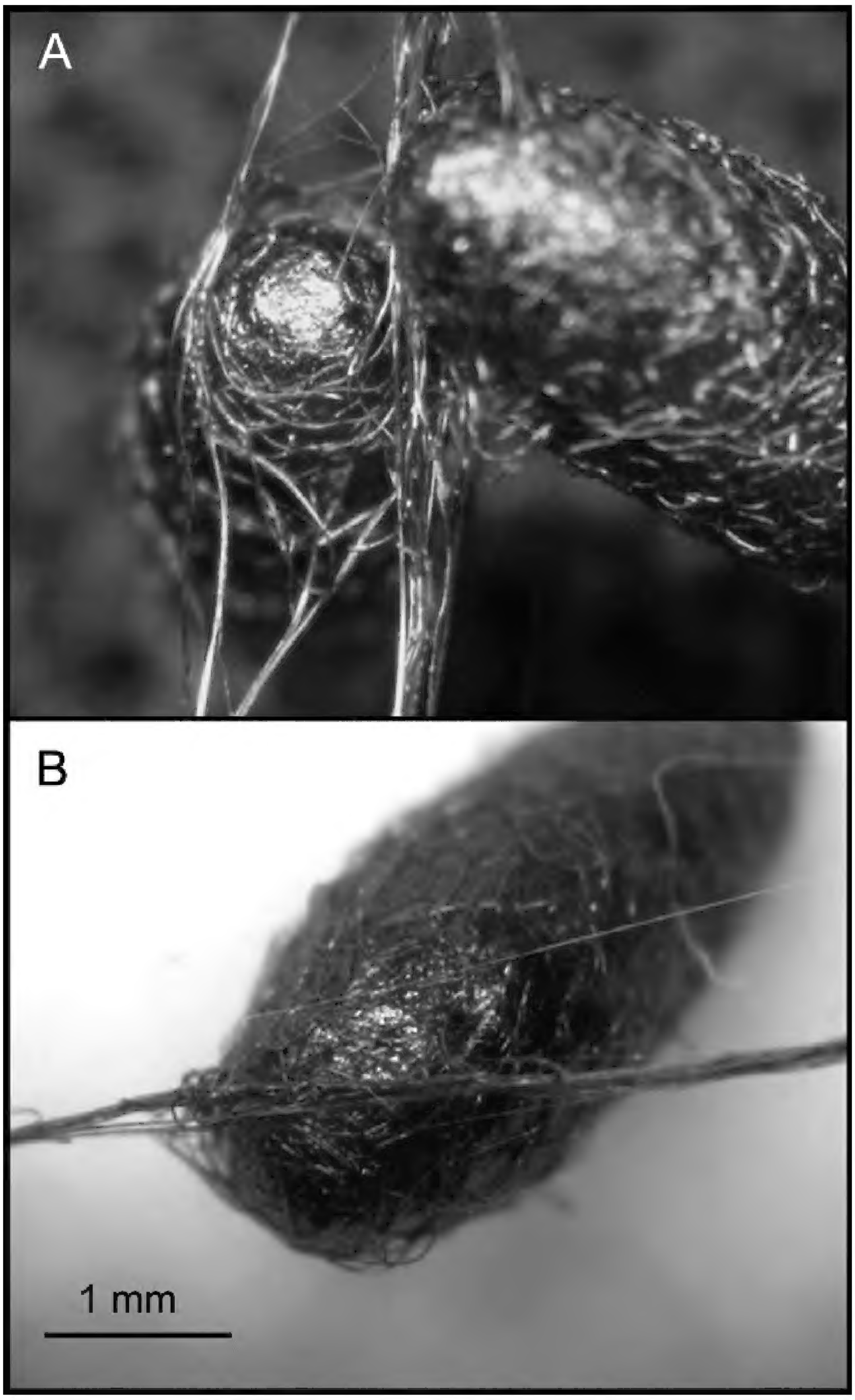

Figure 4. Cocoons attached by the posterior end to the cable. **A** A circle of relatively thick threads secure the cocoon to the cable **B** Cocoon attached to the cable.

wasps were females and eight were males. This sex ratio significantly differed from a 1:1 proportion ($p = 0.011$, Binomial test). Pupae were not hyperparasitized; the only wasp that did not emerge was completely developed and the cause of its failure to emerge was unknown.

Discussion

The cocoons of *Meteorus restionis* sp. n. differ in several respects from those described for other species (Zitani et al. 1998). Most *Meteorus* species are solitary and conse-

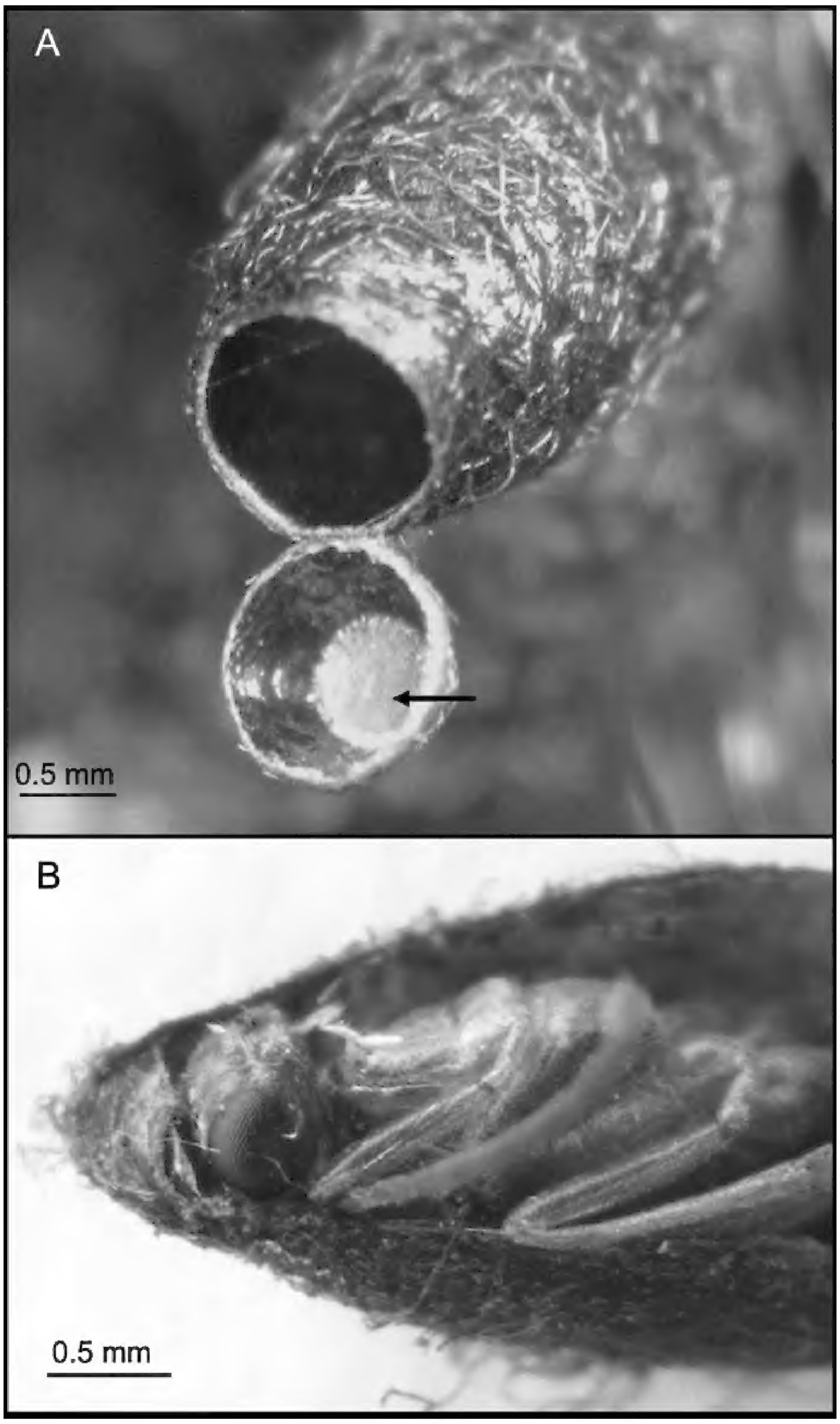

Figure 5. Cap of the cocoon and pupating wasp. **A** The cap finely cut by the wasp hangs from a few threads to the rest of the cocoon. The bottom of the cap is covered by a soft yellowish pad **B** Position of the pupating wasp inside the cocoon; the top of the wasp's head rests on the pad.

quently only one larva emerge from a single host larva (Bell et al. 2000; Zitani et al. 1997, 1998; Balduf 1969; Shaw and Jones 2009). Other species are gregarious and the number of parasite larvae that emerge from a single host larva vary largely (Shaw and Nishida 2005; Bell et al. 2000; Zitani et al. 1997, 1998). Larvae of most gregarious species that parasitize exophytic caterpillars construct their cocoons near or around their host larva producing clusters of cocoons attached individually to the lower surface of leaves by short threads (Zitani et al. 1997, 1998; Shaw and Nishida 2005). Some gregarious species of *Meteorus* also construct relatively complex woollier cocoons in host retreats underground (Maetô 1989; Shaw et al. 2009). The group formed by independent cocoons of *M. restionis* at the end of a long suspended cable and the

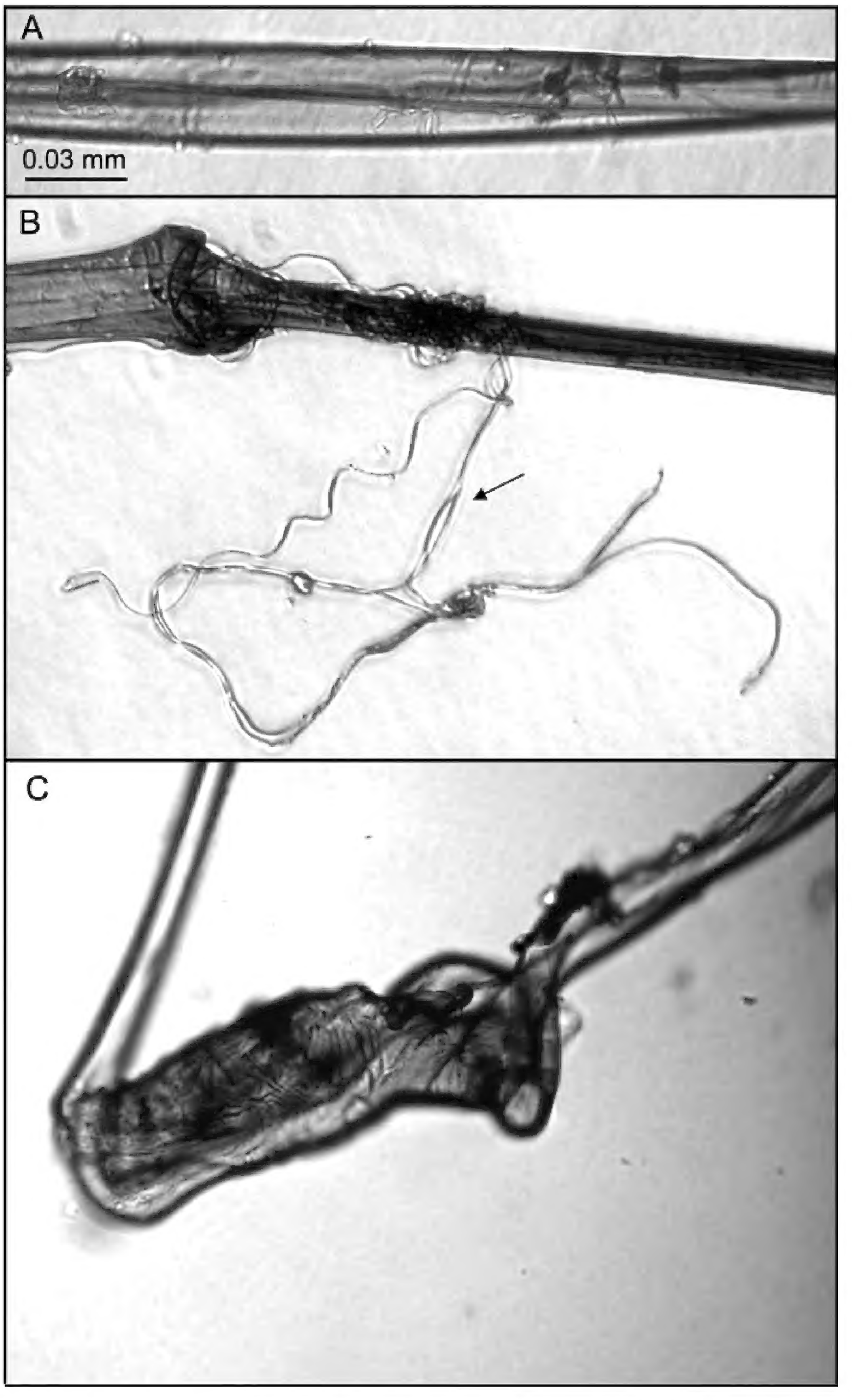

Figure 6. Details of the threads and resin-like clog. **A** A pair of relatively thick threads, possibly produced by a single larva, glued together **B** The threads consist of a large number of fibrils **C** Clog of a resin-like substance. Clogs bind together threads along the cable.

perpendicular arrangement of the cocoons along this cable have not previously been observed in other species of this genus.

The construction of such a cable seems to require that all larvae begin to construct the cocoon approximately at the same time, that each larva somehow twists its individual long thread with other larvae's threads, and glue its thread at irregular intervals with some other threads. Hence, twisting the threads and gluing them together indicate some degree of cooperation, or at least some degree of tolerance, that results in the

construction of a single cable, more resistant to environmental stress. Both tolerance and some degree of cooperation, which not always include coordinated actions (see Wilson 2000 for definition), are considered the initial steps in the evolution of societies in larvae of Lepidoptera and spiders during web construction and maintenance in tent caterpillars and spiderlings (Aviles 1997; Costa 2006). Other species of *Meteorus*, such as *M. komensis*, have possibly a higher level of cooperation in the construction of a communal cocoon (Zitani and Shaw 2002). This places *M. restionis* at an intermediate level of cooperation, between gregarious species that construct individual cocoons and more cooperative species that construct communal cocoons with shared outer envelopes.

Gluing and binding the threads to form a cable and attaching each individual cocoon to this cable, rather than to each individual thread, presumably gives the cocoon additional resistance against wind, rain, other environmental stress, and against possible impacts of flying animals. It is also possible that long threads give better protection against ants or other crawling predators (Zitani and Shaw 2002). However, a single long thread probably increases the effect of environmental stress, such as wind dragging and the probability of being impacted if cocoons are constructed in the path of flying animals. These negative factors may be counteracted by combining individual long threads in a single cable.

Internally, cocoons of *M. restionis* look very similar to those of other species (Zitani and Shaw 2002; Shaw 2006). They have a brilliant, dark solid wall that seems a good protection against some predators and hyperparasitoids; though in other *Meteorus* species some hyperparasitoids are capable of breaking this barrier (Zitani and Shaw 2002). Another internal element of the cocoon of *M. restionis* is the yellow silky pad at its anterior extreme. This pad seems to be strongly developed in possibly those *Meteorus* species that pupate (head down) in suspended cocoons (M. R. Shaw pers. comm.), and it is possibly a characteristic of the entire subfamily. In *M. restionis* this pad has the consistency of compacted cotton. The function of this pad is unknown, but it likely cushions the soft, fresh pupa's head, as the cocoons are slanted, anteriorly downward.

The biology of *M. restionis* brings further information to the understanding of the evolution of the apparent cooperative behavior associated to the construction of complex cocoons in the genus *Meteorus*. However, only a phylogenetic analysis will provide the opportunity to understand the evolution of cooperative behavior within this cosmopolitan genus (Shaw 2006).

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